FORM AND HABIT IN SPECIES OF MALLEUS (INCLUDING THE "HAMMER OYSTERS") WITH COMPARATIVE OBSERVA- TIONS ON ISOGNOMON ISOGNOMON

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Probably no tropical bivalve shells have been better known than those of the well-named "hammer oysters." The black species appears as *Ostrea malleus* in the 10th edition of the *Systema naturae* of Linnaeus. The genus *Malleus* was erected by Lamarck in 1799 for the inclusion of this species and later for the white *M. albus*. These shells were highly prized by early collectors; Dance (1966) records the sale of shells of *M. malleus* for 32 guilders in Holland and 240 francs in Paris during the eighteenth century. The distinctive, indeed exaggerated, hammer shape of these two species has not proved characteristic of the genus (as defined by Thiele (1935)) unless those smaller species without the anterior and posterior extensions of the hinge line be placed in separate genera, such as *Parimalleus* (Iredale, 1939).

Despite long knowledge of and interest in the shells, effectively nothing is known about the mode of life of any species of *Malleus*. Coming from coral reef areas they have been regarded as being attached to them. Thus Iredale (1939) in his account of the bivalves collected during the course of the Great Barrier Reef Expedition refers to *M. malleus* as an inhabitant of coral reefs but states that *M. albus* is not a reef shell but "the mainland species." Although some account of the structure of species of *Malleus* has been given by Pelseneer (1911) and Kühnelt (1938), no one appears ever to have observed these animals in life.

Personal opportunity of so doing was afforded during the sixth cruise of the Stanford University Research vessel "Te Vega" which the author accompanied from Singapore to the Solomon Islands from January to March, 1965. Some additional, and very valuable, information was obtained during some four weeks spent on the Belgian "De Moor" Expedition to the Great Barrier Reef of Australia during September to October, 1967. Acknowledgments for these facilities are given later.

Detailed examination of the smaller, *M. regula* (Forskål), without extended hinge line, provided the basis for conclusions on the adaptations and habitats of *M. malleus* (Linn.) and *M. albus* Lam., specimens of which were obtained from various sources and which undoubtedly represent successively further stages in adaptive evolution, essentially from epifaunal to infaunal life. The striking fact that *M. regula* may occur in vast numbers mingled with similar populations of *Isognomon isognomon* (Linn.), a species of a not very closely related genus which has also taken to vertical posture after byssal attachment, involved an illuminating parallel study. Both species exhibit most interesting consequences of the mono-

EXPLANATION OF LETTERING

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A	anus	MI	mantle isthmus
ABR	anterior byssal retractor	ML	multivincular ligament
AD	adductor	N	limit of nacreous region
AE	anterior extension of shell	OBG	opening of byssal gland
AF	accessory foot	OCL	outer calcareous layer
AOL	anterior outer ligament layer	OF	outer fold of mantle margin
AOM	epithelium secreting anterior outer ligament	P	periostracum
		PAR	pallial retractor
AU	auricle	PBR	posterior byssal retractor
BG	byssal groove	PC	pericardium
BN	byssal notch	PE	posterior extension of shell
By	byssus	PMC	promyal chamber
CT	ctenidium	POL	posterior outer ligament
E	exhalant current	POM	epithelium secreting posterior outer ligament
F	foot		
FL	fusion layer	PR	prismatic layer
I	inhalant current	R	rectum
ICL	inner calcareous layer	RI	ridge associated with pallial retractor
IF	inner fold of mantle margin		
IL	inner ligament layer	U	umbo
LP	labial palp	V	ventricle
MF	middle fold of mantle margin		
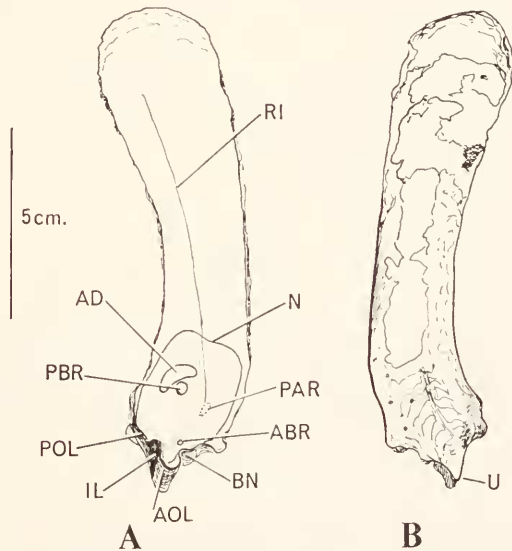
FIGURE 1. *Malleus regula,* right valve, **A**, inner, **B**, outer view. For explanation of lettering in this and all other figures see above.

myarian condition, description and discussion of which supplement a series of prior studies on other monomyarians.

The above statement explains the general plan of this paper in which descriptions of structure, illuminated where possible by discussion of function, precede an account of mode of life and general biology.

The Genus Malleus Lamarck 1799

Malleus regula (Forskål)

This species, widely distributed and very common in the tropical Indo-Pacific, was first personally observed at Palau Gaya, one of a half-circle of three precipitous islands forming the remains of the rim of a large extinct, now flooded, volcanic crater in Darvel Bay on the east of Sabah (North Borneo) which was visited on the *Te Vega* at the end of January, 1965.

Shell

This is straight (Fig. 1), about four times as long as it is broad and attains lengths of some 12 cm. Old shells tend to be very irregular with the outer surface (Fig. 1B) usually covered with calcareous algae and other encrusting growths. It stands more or less erect, firmly attached by byssus threads to a rocky, often partially mud-covered, surface. The prominent posteriorly directed umbones (U) are situated immediately on the posterior side of the byssal notch (BN). These mid-dorsal structures thus lie in the middle of the topographically under surface. This is true of all the species considered (including *I. isognomon*), which for this reason are figured with the umbonal (*i.e.,* "dorsal"), as well as the byssal (*i.e.,* "ventral"), surface undermost as they invariably occur in life.

The internal surface of the shell valve is shown in Figure 1A, and that of *M. malleus* in Figure 3. The nacreous or proximal area (delimited by N) occupies some quarter of the surface, the distal remainder (apart from some thin superficial periostracum) consisting of prismatic (outer calcareous) layer formed by the mantle margins. Conditions are precisely as in *Pinna* (Yonge, 1953b). In both, the mantle is capable of great extension, and corresponding withdrawal, and is able to make rapid repair following the frequent damage species of both genera experience. Within the space occupied by the visceropedal mass (where the nacreous, *i.e.,* inner calcareous, shell layer is secreted by the mantle) lie the scars of the somewhat crescentic adductor (AD) and of the larger posterior and the smaller anterior byssal retractors (PBR, ABR). There is also the fainter scar of the pallial retractor (PAR). From this a low ridge (RI) runs along the prismatic (topographically upper) extension of the shell dividing this lengthways into anterior and posterior regions, corresponding, as shown in Figure 2A, to inhalant and exhalant regions, the former twice as wide as the latter.

Ligament

As shown in more detail in Figure 2A (also in figures of *M. malleus* and *M. albus*) this consists of a centrally placed convex inner layer (IL) secreted by the mantle isthmus (MI) with a shorter anterior, and a longer posterior, outer layer (AOL, POL) secreted in the embayments by the outer surface of the outer fold of the mantle margins. Progressive stages in the growth of the ligament are shown in Figure 2 indicating "ventralward" displacement of the hinge line which is characteristic of cemented bivalves [*e.g., Hinnites, Spondylus, Etheria, etc.* (Yonge, 1951, 1962)] and would seem to be due in the case of this byssally attached species to a similar close adherence of the hinge region to a rock surface. In other byssally attached bivalves, *e.g.,* the Mytilidae, the hinge is not pressed against the substrate.

The ligament is bounded anteriorly on the right valve by the deep byssal notch (Fig. 1, BN). Further reference to the ligament is made in the accounts of *M. malleus* and *M. albus*.

Mantle cavity

The appearance of the animal when fully expanded after removal of the left shell valve and the mantle lobe is shown in Figure 2A. The extent of the nacreous layer within which lies the relatively small visceropedal mass is indicated by the broken line (N). The mantle lobes have extended above this carrying the ctenidia (CT) with them to fill the prismatic extension. Any stimulus causes contraction of the pallial retractor (PAR), the presence of which was first noted by Pelseneer (1911), and consequent withdrawal of the mantle lobes, if complete then within the confines of the nacreous region. There is no pallial line in these monomyarians. Of the three marginal folds, the outer one (Fig. 2B, OF), which secretes an extremely thin but very elastic periostracum (P) as well as the prismatic layer (PR), is obscured by the larger middle fold (MF) which bears a single row of small tentacles as does the better developed inner fold (IF) where they are alternately larger and smaller. By apposition or separation these inner folds, or pallial curtains, control entrance into or exit from the mantle cavity.

The lobes are nowhere fused although closely applied to one another at the tips of the ctenidia somewhat to the posterior side of the end of the distal extension (Fig. 2A). This represents the point of division between inhalant and exhalant chambers. The functional advantage of a wide inhalant region, well raised above the bottom and extending along both anterior and distal surfaces, is apparent.

Promyal chamber

In addition to the extensive exhalant chamber distal to the adductor, water also passes posteriorly by way of a promyal chamber (PMC) corresponding to that initially described in *Crassostrea* by Nelson (1938) and now realized as one of the distinctive characters of that genus compared with *Ostrea*. It represents a secondary connection, on the dorsal side of the adductor, between the anterior and posterior ends of the mantle cavity and, as in *Crassostrea*, runs along the right side. After passage through the ctenidia, the flow of water, along the course indicated by the broken arrows in Figure 2, is assisted by cilia lining the chamber and facilitated by displacement of the rectum to the left side as described and figured by Pelseneer (1911) although without knowledge of its significance. Extrusion is then direct (Fig. 2A, E_1) or, if the mantle margins are applied in this region, in more distal regions of the exhalant chamber.

Nelson pointed out that the promyal chamber in *Crassostrea* increased the pumping rate and also permitted life in greater concentrations of sediment. He correlated its presence with greater elongation in *Crassostrea* and consequent greater distance between the hinge line and the adductor compared with the more rounded *Ostrea*. All of these arguments apply equally to *Malleus,* particularly the last although, as noted later, there is no promyal chamber in the effectively equally elongated *Isognomon isognomon*. The chamber in *M. regula* and *M. malleus* is relatively smaller than in *Crassostrea* owing to the presence of the large
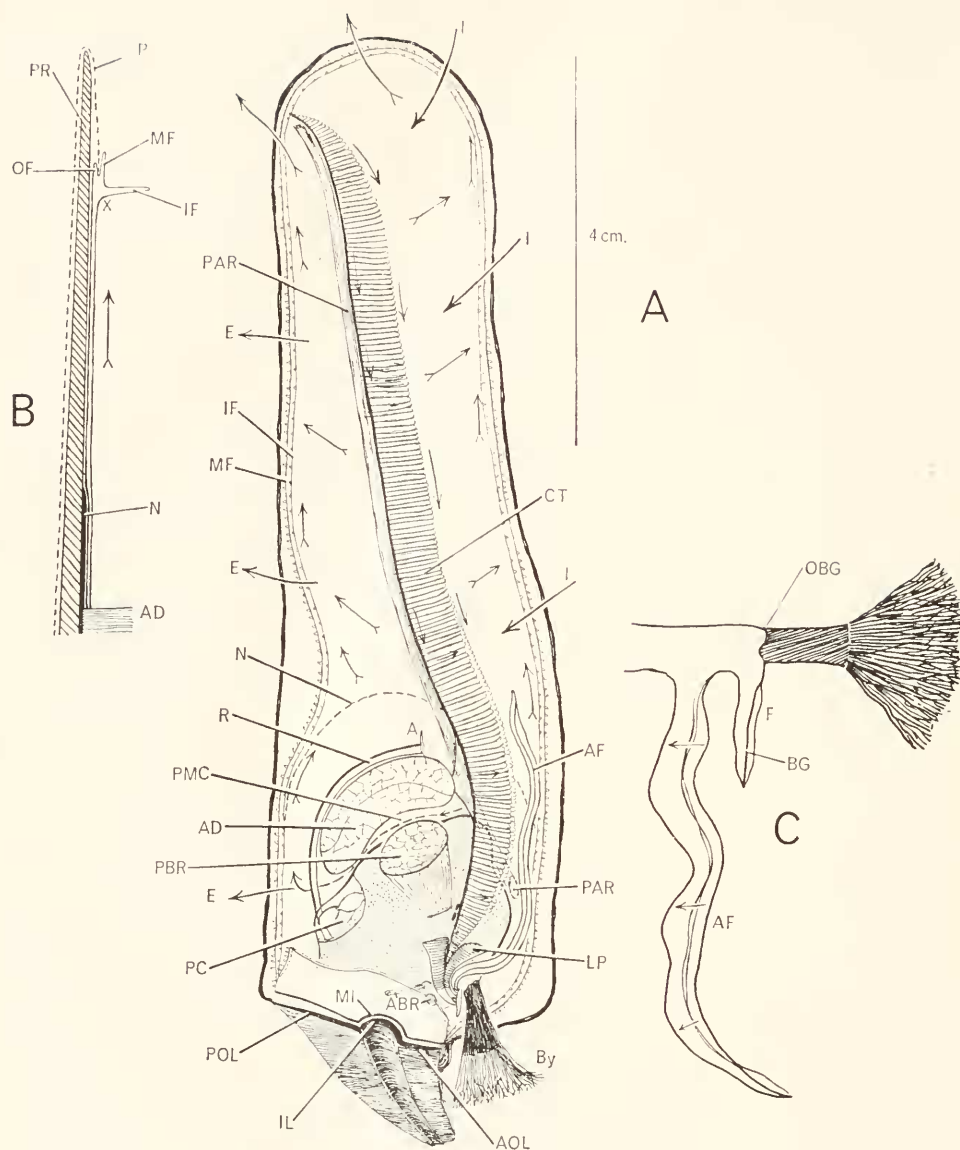
FIGURE 2. *M. regula*. **A**, fully expanded animal within right valve, left mantle lobe removed. Plain arrows indicate direction of collecting currents on the ctenidia, also of inhalant currents; feathered arrows direction of cleansing currents. **B**. Section through valve and mantle distal to adductor showing three marginal mantle folds with periostracum (broken line), outer prismatic layer (oblique lines) and inner nacreous layer (black) of the valve. Waste material carried marginally and then, where marked with x, conveyed distally. **C**, foot, with byssal groove and byssus, and accessory foot viewed laterally. Arrows indicate direction of ciliary beat on extremely active accessory foot.

posterior byssal retractor (PBR) absent in the Ostreidae (and also in adult
M. albus).

Ctenidia and palps

The greatly extended filibranch ctenidia are attached proximally by way of a
suspensory membrane to the anterior surface of the adductor (Fig. 2A) and at
the distal extremities to the inner fold of the mantle margins. Attachments be-
tween the inner demibranchs and between the outer demibranchs are all by way of
interlocking cilia as in other Pteriacea including *Pinna* (Yonge, 1953b). The
structure of the gill in *M. malleus* and *M. albus* is described by Ridewood (1903)
and Atkins (1936, 1937, 1943) although, despite statements to the contrary, the
ctenidium is heterorhabdic with principal filaments. There is fusion between fila-
ments in the region of the "ventral" margins but not terminally. Cilia on the
frontal surfaces beat "ventralward" except for those on the inner surface of the
outer demibranch which beat towards the axis. There are five oralward currents,
three "dorsal" and two "ventral," although there is only a groove along the margin
of the inner demibranch. No evidence of antagonistic frontal currents, such as
Atkins (1936) found in the related *Pteria,* was noted. There are both longi-
tudinal muscles in the axis and lateral longitudinal muscles on either side as
described and figured by Atkins (1943). They must function in co-ordination
with the pallial retractor.

The rather small, rather elongate palps (LP) call for no comment. They are
symmetrical on the two sides and without fusion of the lips such as occurs in certain
Pectinacea. The mouth is relatively large.

Foot and retractors

As described and figured by Pelseneer (1911), the foot in *Malleus* is unique
in being divided into two portions. Both project anteriorly and are ventrally
grooved; the first is elongated, the more distal bears the byssal opening. The
former, designated "bandförmigen Tentakel," was found by Kühnelt (1938) in
M. albus and considered a possible taste organ. It is here termed the accessory
foot (AF) and observations in life have extended knowledge and provided better
understanding of possible function.

As shown in Figures 2A and C, the foot (F) is concerned exclusively with the
planting of byssus threads which issue from the opening of the byssal gland (OBG)
and are directed along the ventral groove. The result is the formation of an
elaborate byssus (By), the threads consolidated basally to form a massive stalk.
This is the sole function of this region in adult life. It could be concerned with
locomotion in early post-larval life as it is in the Mytilidae; it retains that function
throughout life in the closely allied *Pinctada* (Herdman, 1904). The bivalve foot
may also be a cleansing organ as in certain cemented genera, *e.g., Spondylus* and
the Chamidae (Yonge, 1967a) and most strikingly in the Anomiacea where the
massive, calcified byssus is planted direct from byssal opening while the elongate
foot is concerned exclusively with cleansing the mantle cavity (becoming locomo-
tory again in the limpet-like *Enigmonia;* Yonge, 1957). In the Pinnidae the foot
is solely concerned with byssal attachment but a unique pallial organ in the *exhalant*

chamber probably clears that region, especially following the frequent damage these vertically disposed bivalves experience (Yonge, 1953b).

In *Malleus* the function of cleansing has been taken over by the extremely long and active accessory foot which moves with complete freedom throughout the lower regions of the inhalant cavity continually turning and twisting, extending and withdrawing. It is grooved "ventrally" and everywhere ciliated but owing to the constant movement it was impossible to follow the direction of beat except on the outer surface where it is always away from the groove. The function of the cilia appears to be to keep the foot clean, not to direct particles in any particular direction. Transverse sections reveal the presence of a thin layer of circular muscle and within this much greater amounts of longitudinal muscle divided into groups by inward-running strands of fine connective tissue. Blood sinuses are numerous, extension is clearly by blood pressure and contraction of circular muscle, retraction by contraction of the longitudinal muscle.

This is a unique structure which cannot be homologized with any part of the divided foot in the Gastropoda. Its presence is to be correlated with the vertical posture in *Malleus* and the danger of sediment accumulations in the restricted pocket at the base of the inhalant chamber with consequent blockage of palps and mouth (see Fig. 2A). Similar dangers to other similarly disposed anisomyarians, *e.g.*, the Pinnidae and *Pedum spondyloideum* which live, respectively, in sand and in cavities within reef-building corals, are met by way of the unique waste canal in the former (Yonge, 1953b) and of a powerful anterior cleansing current through the byssal notch in the latter (Yonge, 1967b). The small anterior and much larger posterior retractor muscles (ABR, PBR) are symmetrically disposed and effectively entirely concerned with the byssus. Movement of the accessory foot is by intrinsic agencies.

Cleansing

The general course of the cleansing currents in the mantle cavity is indicated by the feathered arrows in Figure 2A. All material in both chambers is carried distally by way of currents running along the inner side of the inner mantle fold (Fig. 2B) and ejected in the distal extremities; there is no accumulation of pseudo-faeces in the inhalant chamber. Cleansing in the base of the inhalant chamber is effected by the accessory foot. Longish faecal pellets discharged from the anus (A) are also conveyed distally for disposal.

Visceropedal mass

Much of this has been described; other anatomical features (shown in Fig. 2A) include the posteriorly disposed pericardium (PC) with the rectum passing through the ventricle and both displaced to the left as described by Pelseneer (1911) in consequence of the development of a promyal chamber. The course of the alimentary canal is simple. The gonad covers most of the visceral mass although all specimens opened—in early February—appeared empty (unlike the associated *Isognomon*), implying recent spawning.

Observations on small individuals

Observations made on animals between 1 and 2 cm. long and up to 6 mm. wide were illuminating. Apart from the byssal notch on the right valve, they are equivalve, almost completely straight-sided and with the prismatic distal region completely plastic and readily bent in any plane. An instance was noted where the distal region had turned at an angle of 90° in the plane of the valves (it could equally be at right angles to this). The adaptive advantage to individuals which may settle under rocks and can only survive by growing around their margins is obvious. The end result is *always* that the distal regions point upward, opening to receive food and oxygen. This region is initially incapable of closure; contraction of the adductor pulls together the rigid nacreous, but not the distal prismatic, region. As in *Pinna,* this shell layer has a high proportion of conchiolin. However, accompanying withdrawal of the mantle lobes will effectively seal the nacreous region. On later relaxation the mantle lobes could be seen, through the translucent shell, slowly "creeping" back into the distal extension. It is probable that the periostracal sheet, which must be stretched during withdrawal, assists this process. Increased growth brings added danger of damage. However the distal shell is capable of indefinite repair (as in the similarly constructed Pinnidae and most strikingly in *M. malleus;* see Fig. 5A) so that larger shells become increasingly irregular while their full exposure leads to overgrowth by encrusting organisms.

Malleus malleus (Linn.)

This is the black hammer oyster, the longest known and best known species. During the cruise of the *Te Vega,* living specimens were obtained from shallow water near Zamboanga in the Philippines and through the kindness of divers from deeper water in the harbor at Rabaul, New Britain. Subsequently others were examined which had been collected by diving off Lizard Island and off Low Isles by Dr. A. Bastin of the *De Moor* Expedition. In all cases the animals came from relatively clean sandy bottoms in which they were largely buried, only the most distal regions projecting. Specimens measured in Rabaul were 18 to 21 cm. long with a "hinge line" up to 21 cm.; in Australia up to 22 cm. long by as much as 24 cm.

The interior of an adult shell is shown in Figure 3E. The general appearance is similar to that in *M. regula* with a relatively smaller nacreous region bearing the same four muscle scars. There is a well developed byssus but here *both* valves are notched, although to a greater depth on the right. The significant difference, apart from the greater extent of the prismatic region distally, is the formation of similar areas in line with the hinge to produce a very long posterior, and a somewhat shorter anterior, extension (PE, AE). It will be noted (Fig. 3) that the nacreous region is *not* concerned in this. The mantle lobes pass into and are withdrawn away from these extensions exactly as they do in the distal region. While the posterior extension does resemble (on an hypertrophied scale) the posterior auricle in a pectinid, this is not true of the anterior extension which is separated from the hinge and ligament by the byssal notch. There is thus no anterior extension of the ligament but this is not true posteriorly as revealed by the transverse sections—actually of *M. regula* but more suitably discussed in
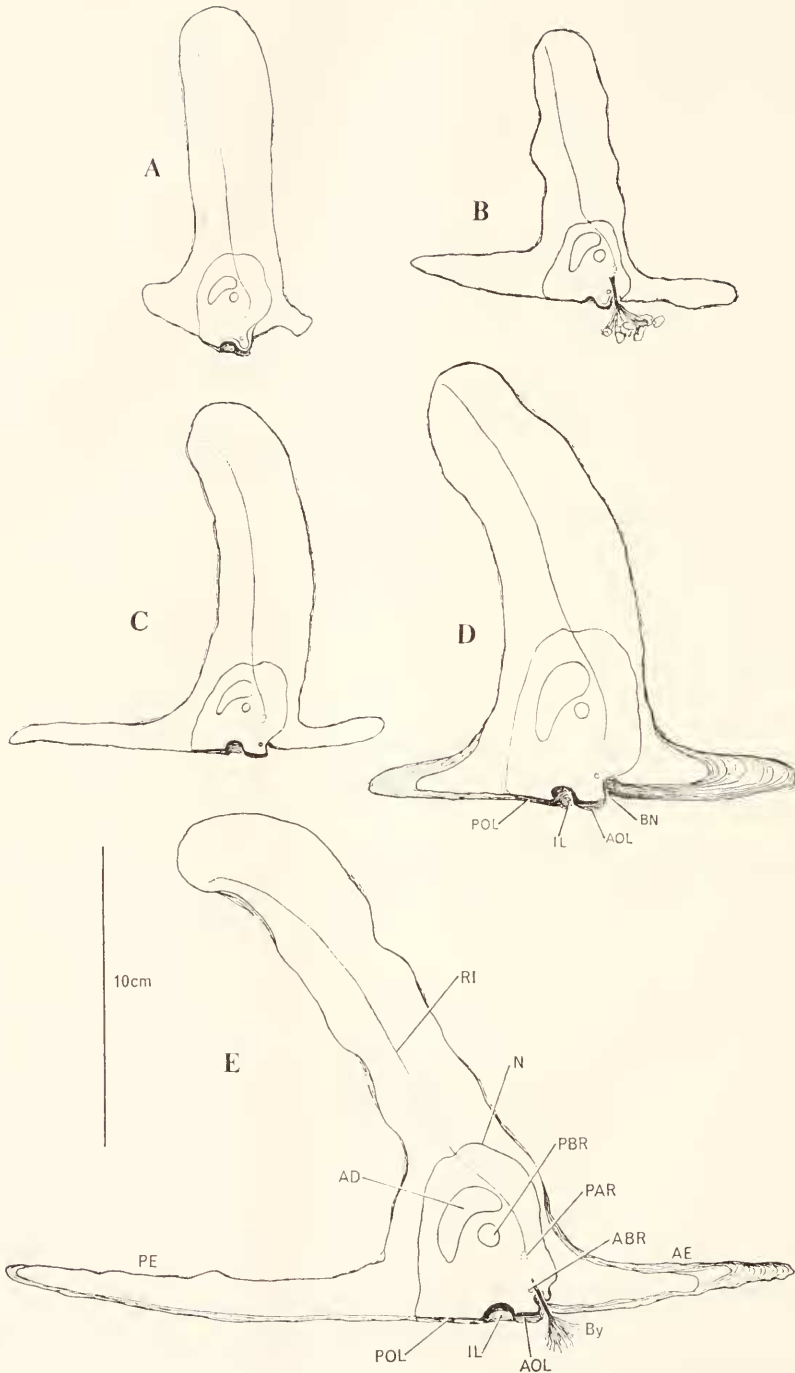
FIGURE 3. *M. malleus,* **A–E**, interior views of right valves showing various stages in growth with full development of anterior and posterior extensions of the "hinge line" shown in adult (**E**).

relation to *M. malleus*—shown in Figure 4. These indicate the structure successively from anterior to posterior (*a-g*) of the anterior outer, the inner and the posterior outer ligament layers (AOL, IL, POL) with their respective secreting epithelia (AOM, MI, POM). There is a posterior movement in growth indicated by the intrusion of the anterior outer layer into the inner layer (*b*, *c*) and a corresponding extension of the latter backward on either side of the posterior outer layer (*f*). Finally, posterior to the primary ligament formed by these three layers (with initially a covering periostracum) there is a secondary extension consisting of fusion layer (*h*, FL) formed by the union of the outer surfaces of the outer fold of the mantle margins, a secreting surface which elsewhere forms the outer calcareous (*i.e.*, prismatic) layer of the valves (OCL). This secondary ligament, short in *M. regula,* is of impressive length in *M. malleus* and *M. albus* (Fig. 6) owing to the great posterior extension of the hinge line in those species. It can have little or no functional significance. It corresponds to the long posterior secondary ligament in the Pinnidae (Yonge, 1953b) which is certainly functionally significant. Both represent the consequence of pallial fusion associated with posterior extension of hinge line.

Apart from the lateral extension of the mantle lobes, internal structure is similar to that of *M. regula.* Interest concentrates on the formation of the lateral extensions of the shell and on habits and life history. As shown in Figure 3, these extensions appear at varying periods in the life history. Thus specimen **A**, although longer than **B**, still has only short extensions. In **B** and **C** the shell has the hammer form and is being vigorously extended in all three directions. In **D**, however, while length increases the lateral pallial extensions have been withdrawn although without effect on the extent of shell earlier secreted. But the mantle could again extend and increase the length of the "hinge line."

The transition from the condition in *M. regula* to that in *M. malleus* clearly occurs during the life history. As discussed later, it permits a changed mode of life. Apart from its vertical disposition, *M. regula* is a typical byssally attached epifaunal bivalve. *M. malleus* is not; it lives in clean but usually coarse sand with the byssus attached to fragments on this (much as does *Pinna*). The anterior and posterior extensions to the hinge line assist in the maintenance of the shell which is always buried with only the distal quarter or less exposed. The extent of exposure is usually revealed by the presence of encrusting organisms absent from buried regions of the shell. The shell extensions provide an anchor within the sand in which this species lives. But the byssus persists throughout life.

The relatively thin shell, the three projecting extremities composed exclusively of prismatic layer with a high proportion of organic conchiolin, inevitably suffers extensive damage. It is rare to find a large shell which does not exhibit extensive areas of repair. An example (from Rabaul) is shown in Figure 5A. The animal has withdrawn from a broken extent of distal shell and formed a new one at a somewhat different angle to the basal extensions, the form of which has also been somewhat altered. Such changes may be in any plane and many adult shells are of grotesquely distorted appearance. The area occupied by the viscero-pedal mass is seldom, if indeed ever, affected. Conditions are precisely as in the Pinnidae, also byssally attached within soft substrates, similarly exposed to damage and with the same means of extensive and rapid repair of these exclusively pris-
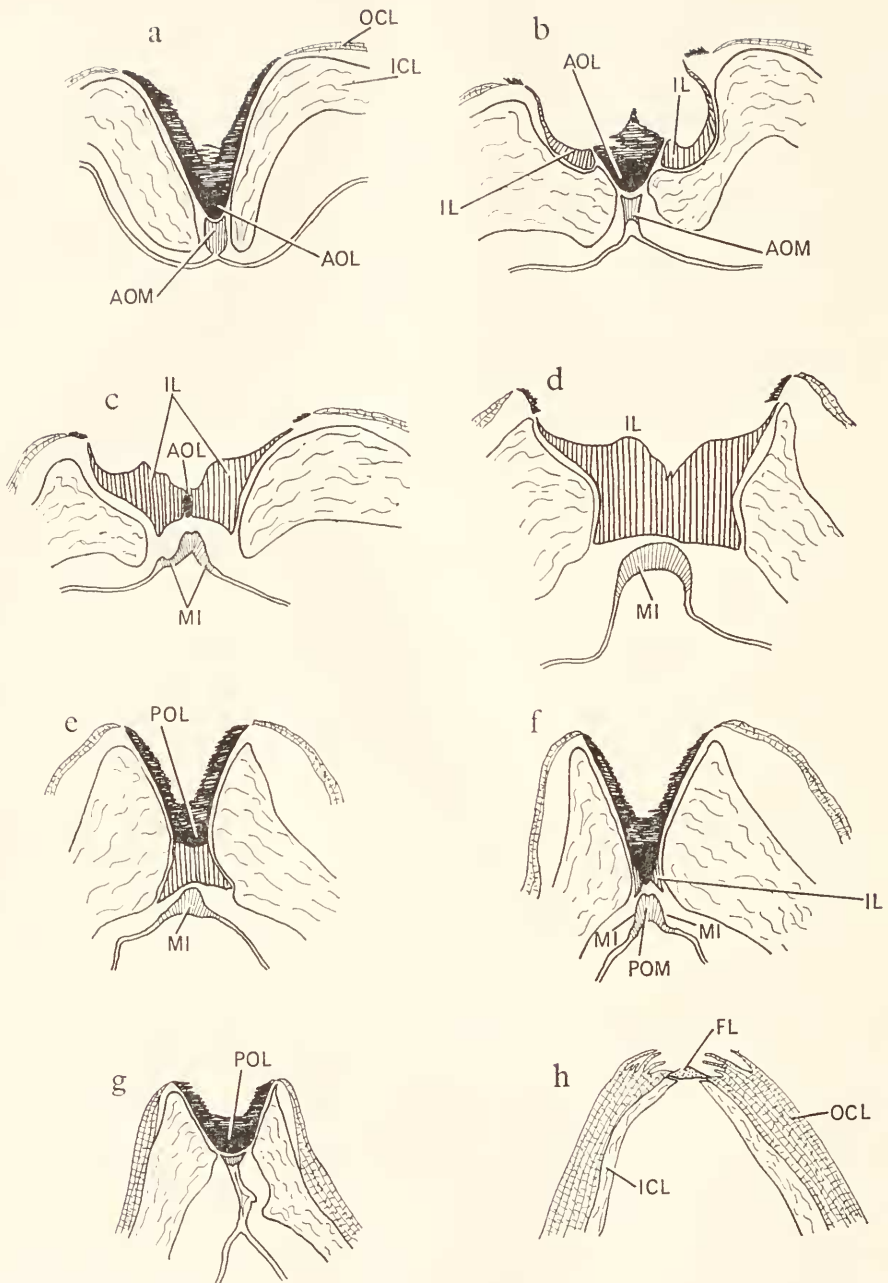
FIGURE 4. *M. regula*. Transverse sections through ligamental region from anterior end back, *a-c* in region of anterior outer ligament; *b-f* in region of inner ligament; *e-g* in region of posterior outer ligament; *h* in region of fusion layer.
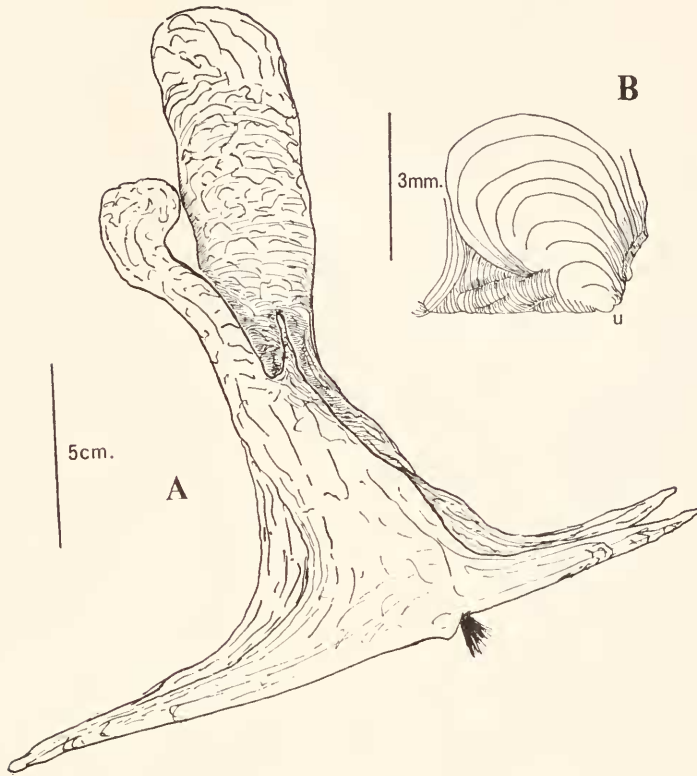
FIGURE 5. *M. malleus,* **A**, very irregular shell (from Rabaul); the mantle lobes have withdrawn from the first formed distal (prismatic) regions of the valves to form new ones at a somewhat different angle to the "hinge line." The nacreous region of the shell is not affected; **B**, umbonal region of left valve showing initial form (resembling *Pinctada*) immediately after settlement (After Jackson, 1890).

matic regions with very high conchiolin content (Bevelander and Benzer, 1948; Bevelander, 1952; Yonge, 1953b).

Malleus albus Lam.

The shell of this second hammer oyster (Fig. 6**A**) differs in being yellowish white and much stouter; the prismatic layer is more heavily calcified. There is less repair and the shells are therefore less irregular. They attain much the same size; the largest measured, from Bougainville in the Solomons, was 24.5 cm. long with a hinge line of 25 cm. Unlike *M. malleus,* the shell margins are deeply folded, the two valves interlocking very precisely. As originally noted by Lamarck, the adult shell lacks a byssal notch and Kühnelt (1938), in a description of a preserved specimen, found neither byssus nor posterior byssal retractor. As shown in Figure 6**A**, the corresponding muscle scar has disappeared, covered over by subsequent secretion of nacreous material.
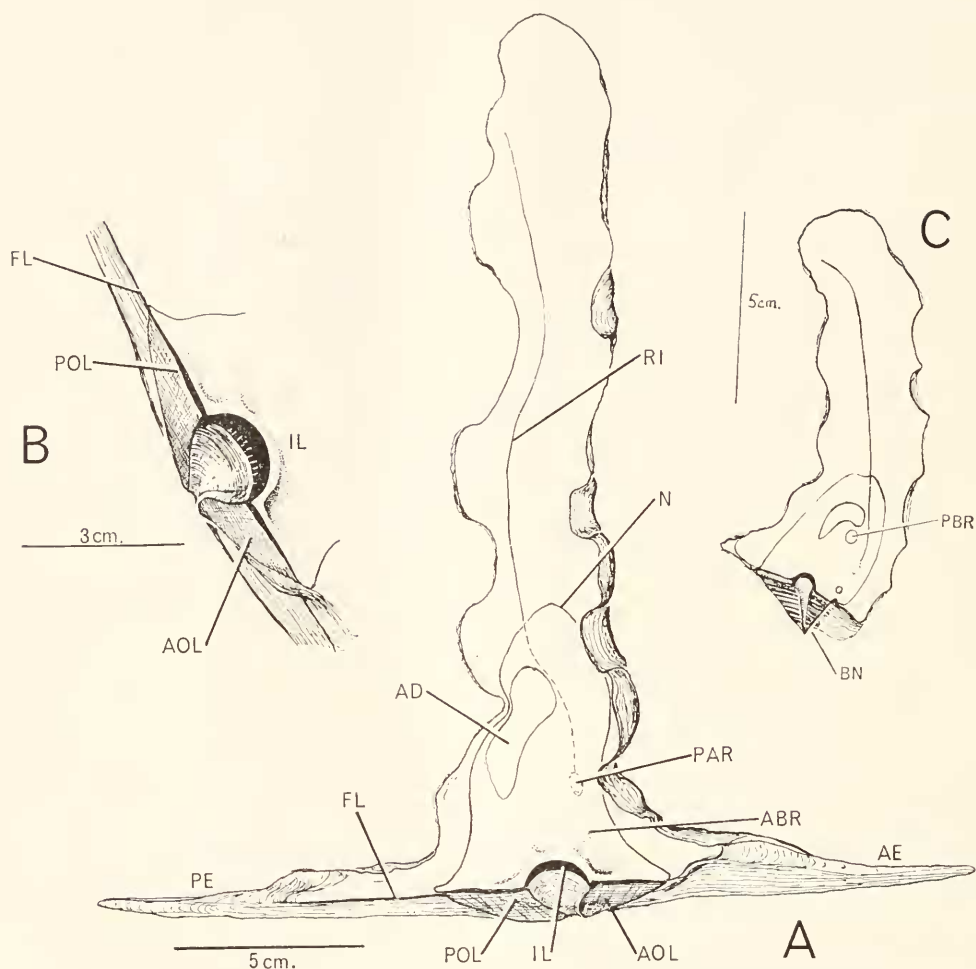
FIGURE 6.   *M. albus.*   **A**, interior of right valve of adult shell; **B**, ligamental region further enlarged; **C**, interior of right valve of half-grown specimen with byssal notch still present.

In a younger shell, at a stage before the hinge line has lengthened (Fig. 6**C**), there is both byssal notch (BN) and muscle scar (PBR).   Unfortunately this shell, which was personally collected at Zamboanga in the Philippines, was empty.   A living adult specimen was later collected by Professor T. F. Goreau by diving under the *De Moor* in the lee of Lizard Island within the Great Barrier Reef. The shell was 16.5 cm. long by some 12 cm. along the hinge line.   There was no byssal notch, no byssus and no posterior byssal retractor although the small anterior muscle was retained.   The true foot was reduced to a small protuberance with a minute opening of the former byssal gland and was situated at the base of the very large and extremely mobile accessory foot.

In *M. albus,* therefore, the animal comes to be anchored exclusively by way of the anterior and posterior extensions of the shell. Moreover it differs from *M. malleus* in living always in a substrate of muddy sand. Initial information to this effect was obtained from shell collectors at Rabaul; this was later confirmed by Mr. S. Bernik of Cairns, N.Q., who had collected specimens from muddy sand at depths of about 30 feet off Bougainville Island. The specimen from Lizard Island came from a similar substrate; it was lying somewhat obliquely with the distal third covered with sponge and other encrusting growths. Specimens of *M. malleus* from that area all came from clean sand.

Life History in the Genus Malleus

In the absence of precise knowledge any discussion about life histories must be on a basis of reasonable supposition. The problem is least in *M. regula;* there the larvae must settle on a rocky surface where mud is present. Unless impeded by overgrowths of rock the shell will then grow vertically. In the two other species metamorphosis of the settling veligers must be stimulated by contact respectively with a clean sandy or sandy gravel substrate or with one of muddy sand. Despite the opinion of Kühnelt, who considers the shell extensions as concerned with stability after attachment to rock, both *M. malleus* and *M. albus* are infaunal. Settlement of the larvae of *M. regula* on mud-covered rock could well represent the ancestral habit.

Initial byssal attachment is presumably to small fragments within the substrate. Gradual descent into this as growth proceeds must initially—as in the Pinnidae—be due to progressively deeper extensions of the foot with planting of new byssus threads on to fragments further down. The progressive extension of the hinge line will certainly anchor the animals more securely but at the same time must present an obstacle (absent in the anteriorly pointed Pinnidae) to the further penetration which certainly occurs. The eventual closure of the byssal notch in *M. albus* will even prevent any downward ejection of water which could assist further penetration in *M. malleus*. However a large shell of *M. albus* could well settle into the softer substrate it inhabits by its own weight. According to Mr. Bernik shells of this species are usually obliquely disposed with two regions of the shell protruding, presumably the posterior as well as the distal extremity. Professor R. D. Purchon (personal communication) states that, near Singapore, he collected living specimens lying on the surface of muddy sand. They could have been thrown up by storms. This does not appear to happen in the attached *M. malleus*. In both species not more than a third (often less) of the distal region projects. Differences in the two infaunal species are certainly associated with their distinct habitats. Water movements will be greater in regions where clean sand or shell sand accumulates. The combined effect of byssal attachment and shell anchorage would seem to be needed; the distorted form of larger shells indicates major disturbances and the means of coping with these. Water movements are obviously less where muddy sediments accumulate—so the byssus can be discarded while a thicker shell will oppose greater resistance to undue settlement of the massive adult shell into this softer substrate.

The Genus Isognomon Solander 1786

This genus, with *Malleus* included by Thiele (1935) in the Family Vulsellidae of the Pteriacea, differs from that genus in the possession of a multivincular type of ligament (Figs. 7, 8, ML). This has been described by Trueman (1954) for *Pedalion (Perna) alata.* (These generic names are synonyms for *Isognomon.*) Instead of the usual single inner ligament with bounding and superficial anterior and posterior outer ligament layers, the ligament is here subdivided into a series of inner ligament layers (or resilifers) with intervening outer ligament layers as shown in Figures 7–9. This type of ligament is shared with only the allied genus *Crenatula* and might be considered, as Trueman points out, to indicate wider than merely generic separation from *Malleus.* However the anatomical studies of Pelseneer (1911), which have been confirmed, do indicate close affinity between *Isognomon* and *Malleus* while Bernard (1898) describes the presence of a minute resilifer in association with the umbones and anterior to the large inner ligament in *Malleus.* By removing the major dissimilarity, this could indicate considerable affinity between *Malleus* and *Isognomon.*
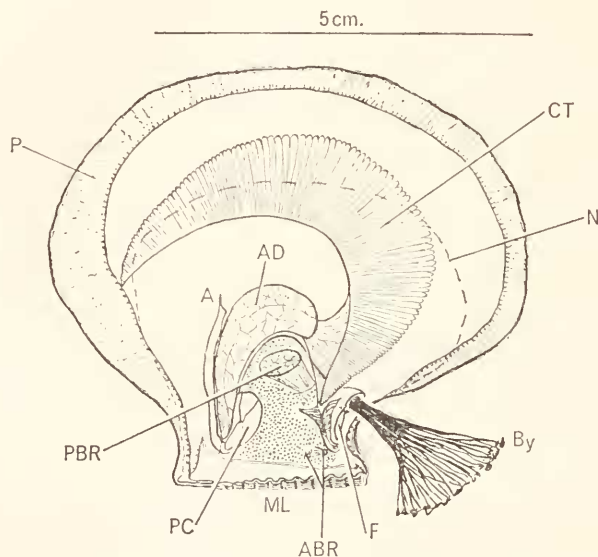

FIGURE 7. *Isognomon ephippium,* general view of animal lying within right valve, left valve and mantle lobe removed. Withdrawal of periostracal sheet formed by outer fold of mantle margin indicated (P).

Isognomon ephippium (Linn.)

A brief account is given of this species (Fig. 7), specimens of which were collected at Kieta on Bougainville Island. The rounded "oyster-like" form is characteristic of the majority of species of this genus which is widely distributed in the tropical Indo-Pacific and Atlantic (where it extends to Bermuda). This description forms a necessary preliminary to the more detailed account of *I. isognomon* where form and habit so closely parallel those in *M. regula.*

This and other rounded species are characteristically attached to rocky, often inter-tidal, surfaces by a massive byssus. This projects through a notch on the right valve on which side the animal lies precisely as do species of the pearl oysters, *Pinctada* and *Pteria* (Pteriidae). The animal has the typical monomyarian form with the viscero-pedal mass reorganized in relation to the centrally placed, although somewhat dorso-ventrally extended, adductor (AD) around which curl the ctenidia (CT). Although the nacreous region (delimited by the broken line N) is relatively larger than in *Malleus,* it is surrounded by a broad marginal prismatic region. The mantle margins retract across this retaining attachment to the edge of the shell by a delicate periostracal sheet (P). The small foot (F) is concerned, probably exclusively, with planting of the massive byssus (By). There are large posterior and small anterior pedal retractors (PBR, ABR) the latter with divided insertions. As shown by Pelseneer (1911) there is no asymmetry in the heart region, *i.e.,* no promyal chamber. As in all such monomyarians there is an extensive inhalant, and a correspondingly restricted exhalant, region. Ciliary currents were not particularly observed in this species; they doubtless correspond to those figured for *I. costellatus* by Stasek (1963) showing rejection of waste particles from both inhalant and exhalant chambers at a common point just on the exhalant side of the tip of the ctenidia.

Isognomon isognomon (Linn.)

This common Indo-Pacific species differs from *I. ephippium* and similar species in being elongated, attached in an erect position and, as noted already by Kühnelt (1938), assuming both the external appearance and mode of life of *M. regula* with which it is found. It is somewhat the larger, attaining lengths of 15 cm. and being somewhat broader. Appearance in life after removal of the left valve and mantle lobe is shown in Figure 8 which is directly comparable with that of *M. regula* (Fig. 2A.) There is obvious difference in the structure of the ligament which in *Isognomon* extends along the entire dorsal surface of the shell and in the position of the byssal notch, here anterior instead of dorsal. Consequently the massive byssus, the threads of which are not basally fused, emerges in that direction although applied to an under surface. The nacreous area is relatively much larger and (*cf.* Figs. 3 and 9) its margins less definite, the mantle lobes with the ctenidia not retracting so far. There is no pallial retractor and no corresponding ridge within the distal region of the shell and no promyal chamber. Without the accessory appendage, the foot is primarily concerned with byssal attachment but still large enough to have possible cleansing functions within the anterior extremity of the mantle cavity.

Distal to the nacreous region the mantle lobes and ctenidia are increasingly pigmented and finally dense black. The mantle margins are as in *Malleus* but thicker and relatively larger with short tentacles on the inner and middle folds. The non-plicate ctenidia are less firmly united and the filaments separate more readily (*i.e.,* are more typically filibranch) than in *M. regula.* As in that species there is no "ventral" groove along the outer demibranch and ciliation is similar. The tips of the ctenidia are attached to the inner mantle folds in the same position as in *Malleus,* the mantle cavity being similarly divided; the exhalant chamber is correspondingly greater than in the rounded *I. ephippium* (*cf.* Figs. 7 and 8).
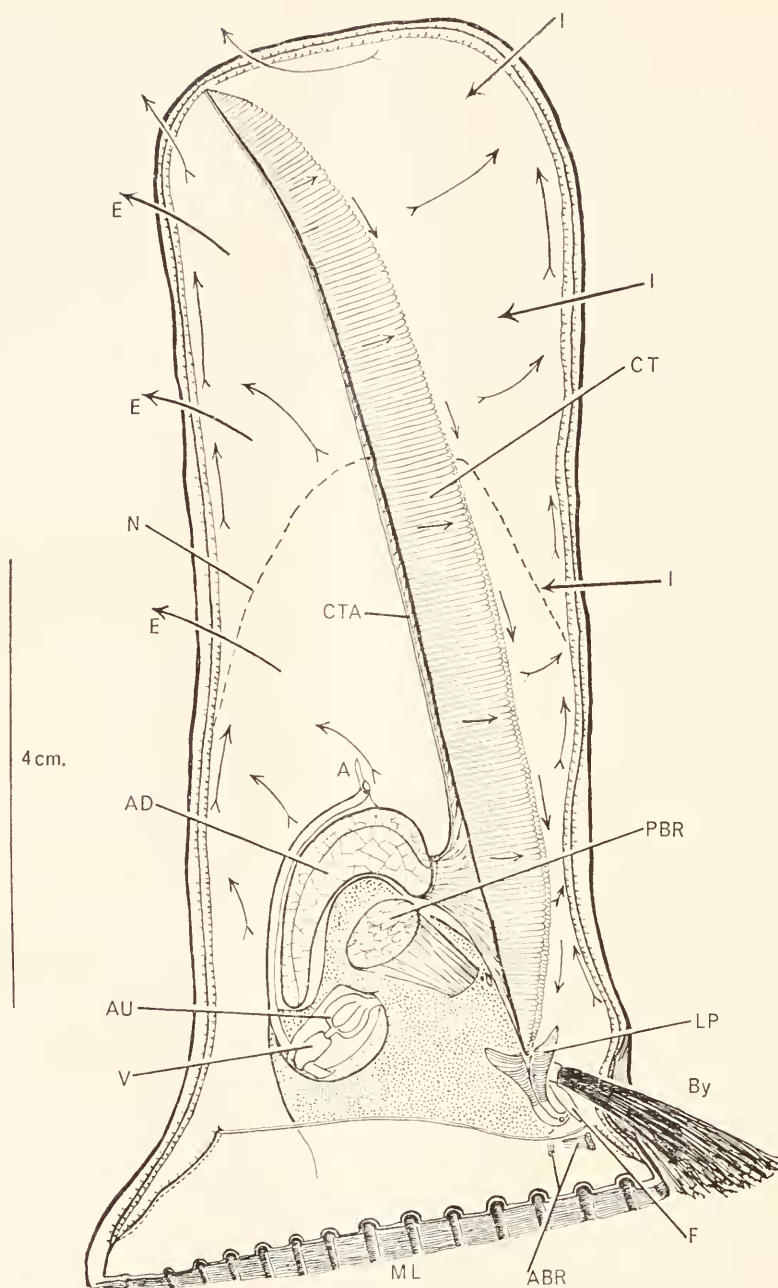
FIGURE 8. *I. isognomon,* fully expanded animal within right valve, left mantle lobe removed. Plain arrows indicate direction of collecting currents on the ctenidia, also of inhalant and exhalant currents; feathered arrows direction of cleansing currents.

The palps are relatively longer than in *M. regula;* the lips are similarly developed, without frilling or fusion. There is a long anal flap which assists in directing the faeces, long scroll-like pellets up to 5 mm. long. As in *Malleus,* all waste material in both inhalant and exhalant chambers is carried to the inner edge of the inner mantle fold and so to the posterior distal regions where it is ejected (see feathered arrows in Figure 8).

Unlike *M. regula,* the gonad, which covers the visceral mass, was obviously maturing although sperm was not ripe.
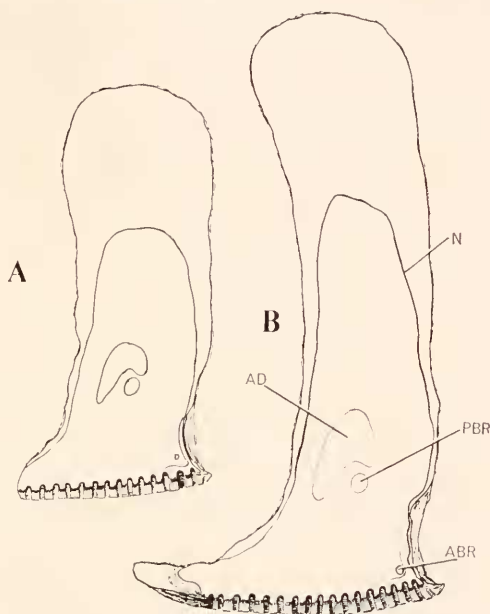
FIGURE 9. *I. isognomon,* **A, B,** interior views of right valves of two specimens showing stages in extension of the ligament and hinge line and of the distal region. The shells are 12 and 17.5 cm. long.

In the smallest animals collected the shell was 13 mm. long by 8 mm. wide and was oval rather than elongated like similar-sized *M. regula.* The shell is usually bluish with light-colored radiating curved rays. Young shells in dark areas tended to remain white. In some the foot was observed extended and seeking a surface for byssal attachment; when found initial threads were quickly secured. Until some 30 mm. long the shells remained oval and then displayed increasing irregularities due to the confined space in which they grew and to the effects of repair. But there is increasing elongation as form changes from the initially more rounded condition. They come to assume a striking external resemblance to *M. regula* although the hinge line is extended posteriorly to a greater extent than in that species (*cf.* Figs. 1 and 9). This process of extension continues until, as shown in Figure 9B, it may attain a length double the width of the shell. At this size the mantle tissues tend to withdraw, the ligament no longer elongates and the shell only increases in thickness.

Multivincular ligament

Two stages in the growth of the ligament are shown in Figure 11**A**, **B**. It begins as a simple opisthodetic ligament (**A**), the inner ligament layer inclined posteriorly from the umbones as in *Malleus*. But instead of this increasing steadily in size by added secretion from the mantle isthmus as in that genus (see Fig. 2**A**), new areas of inner ligament, or resilifers, appear at intervals posteriorly. Two of these are shown in Figure 11**B**; the maximum number observed in *I. isognomon* was 18. While obviously the number is related to the length of the hinge line, it is not necessarily related to the length of the shell.
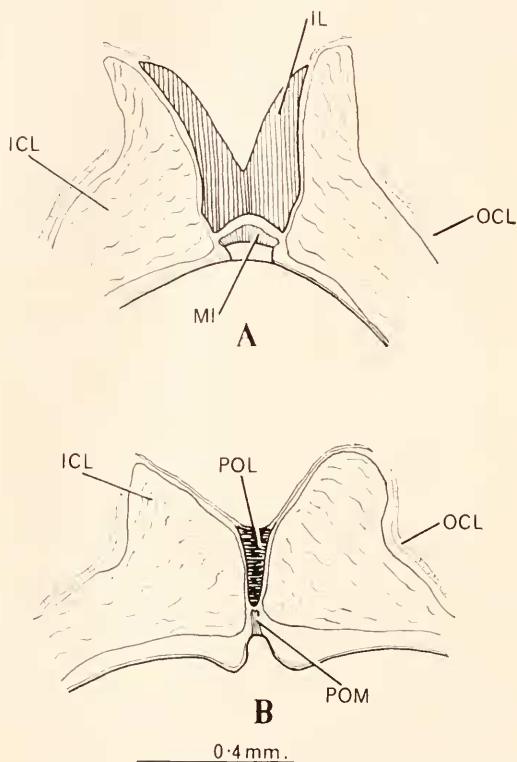

FIGURE 10. *I. isognomon*, transverse sections through ligament, **A**, through a region of inner ligament (a resilifer) ; **B**, region of outer ligament between resilifers.

In older individuals the original resilifer may be partially worn away or lost. Trueman (1954) describes a fusion layer but no sign of this appears in sections nor, in view of the absence of any extension of the mantle behind the primary ligament, as occurs in *Malleus* and *Pinna*, would its presence seem possible. The unsolved problem in this type of ligament is the origin of the successive areas of inner ligament, the one first formed being secreted by the mantle. Although there is as yet no certain supporting evidence, it appears most probable, as indicated diagrammatically in Figure 11**C**, that successive regions of the inner mantle surface

(which normally secretes the inner calcareous, *i.e.*, nacreous, layer of the valves) fuse in the mid-line to invade the epithelia secreting the outer ligament layer and produce successive mantle isthmuses which secrete resilifer 2, then 3 and so on posteriorly. The inner mantle epithelium is here assumed to have the potential of secreting inner ligament should it, like the original mantle isthmus, become situated in the mid-dorsal line, *i.e.*, when subjected to the opening and closing movements of the valves. As in *Malleus* there is a marked ventralward movement of the hinge line as shown in the transverse sections (Fig. 10).
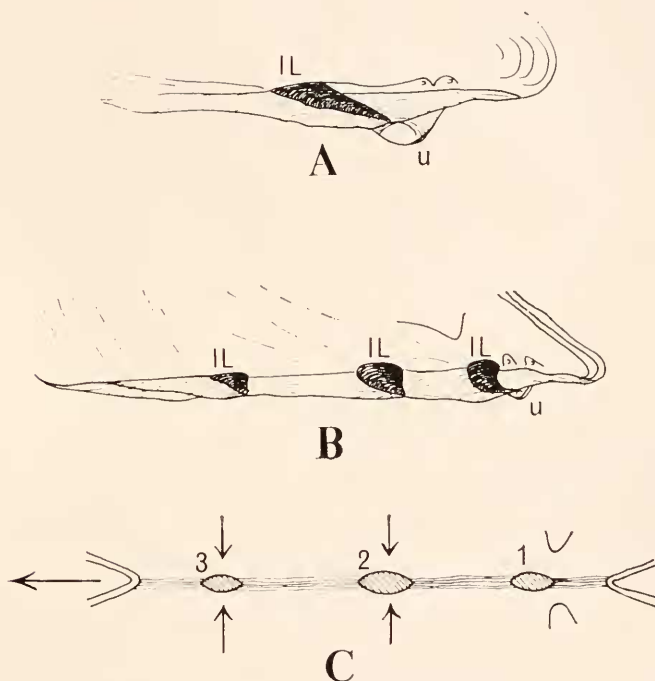

FIGURE 11. *I. ephippium*, views of ligamental regions of young shells (right valves), **A**, with only the original region of inner ligament; **B**, with two others formed subsequently (both from Jackson, 1890); **C**, diagram indicating possible mode of formation of multivincular ligament, 1–3 successively formed resilifers (1 in association with umbones), arrows indicate regions of possible cross fusion of inner mantle epithelium, horizontal arrow direction of ligamental growth (original).

MIXED NATURAL BED OF M. REGULA AND I. ISOGNOMON

A remarkable mixed population of *M. regula* and *I. isognomon* was encountered in the narrow and very shallow channel between Palau Gaya and the much smaller Palau Tatagan. The general appearance of this "clam bed" at low spring tide is shown in Figure 12**A** with a closer view in Figure 12**B**.

The shallow rocky channel was everywhere covered with the densest possible growth of mixed *M. regula* and *I. isognomon*. The upright shells formed a compact "pavement" over an area of some 65 by 40 meters kept free by water move-

Figure 12. **A**, passage between Palau Tatagan and Palau Gaya photographed from south at low spring tide and showing exposed bed of mixed *Malleus regula* and *I. isognomon;* **B**, closer view of an area of the bed largely exposed and showing density of the mixed population.

ments from mud or sand.   The maximum population counted within a foot square patch was 97, the largest *M. regula* being 12 cm. and *I. isognomon* 15 cm. long.   The shells were usually irregular, due to dense crowding and frequent repair, but all pointed upward.   Although the rock surface was irregular, all was smoothed out by the zonal growth of these bivalves above which occasional rocky patches projected.

As the tide exposed them sudden contractions of the "quick" muscle of the adductors produced innumerable jets of water (Fig. 12B).   These ejections could be cleansing or be related to stages in mantle withdrawal.   A final tightening up due to contraction of the "catch" muscle and the shells remained firmly closed until again covered with water.

Examination of samples indicated a greater proportion of *Malleus* in higher, and of *Isognomon* in lower, levels.   In areas first uncovered proportions were almost 4/1, in mid and lower levels they were almost 1/1 but in the deepest level sampled, they were 1/3.   Three factors could account for these slight differences in horizontal distribution; (1) tolerance to exposure (*i.e.,* effects of temperature and desiccation); (2) tolerance to presence of mud; (3) level at which the larvae settle.   However the striking fact is not these minor differences but the complete mingling of two distinct species in the one habitat.

The bed constituted an interesting ecosystem.   Within the shelter provided by the upright shells was a varied community of attached and free-living animals such as mussels, small cowries, crabs and weed with numerous ophiuroids moving actively between the bases of the shells.   Occasional *Pinna* sp. were found in this unusual environment.   Attached to the occasional patches of exposed rock was a distinct population of oysters, patelloid limpets, *Chama* sp., etc.

Evolution Within the Pteriacea

This group is more open to criticism than are the other four superfamilies—Mytilacea, Pectinacea, Anomiacea and Ostreacea—into which Thiele (1935) divided the Order Anisomyaria.   Of the three constituent families, two genera of the Vulsellidae possess a multivincular ligament (but see Bernard, 1898), and so might be included in a separate family, while the heteromyarian Pinnidae have many unique features (Yonge, 1953b) and could be separated as a distinct Superfamily.   However, accepting the present position, in Table I are listed certain crucial characters of the constituent genera with particular reference to habitat.

The Pteriacea occupy three distinct habitats: (1) a certainly primitive one byssally attached to rock or other hard surfaces, and secondary ones (2) without byssus within sponges (and also algae) and (3) with byssus in soft substrates although with eventual loss of this in *M. albus*.   There is thus a tendency, absent in all other Anisomyaria, for return to infaunal life (the exception would be rock-boring Mytilacea, *e.g., Botula* and *Lithophaga*).   It could be noted in possible defense of the present classification, that both the alivincular *Vulsella* and the multivincular *Crenatula* live in sponges, and both *M. malleus* with *M. albus* and the Pinnidae occupy soft substrates.

These points are illustrated in Figure 13.   From the primitive habit of byssal attachment with the animal lying on the right side found in the Pteriidae (*e.g., Pinctada*) and also in most species of *Isognomon* (**A**) there is change to the

vertical posture found in *I. isognomon* (**B**) and *M. regula* (**C**). From the latter condition comes invasion of soft substrates with accompanying elongation of the hinge line in *M. malleus* (**D**) and *M. albus* (**E**), the second losing the byssus in adult life. From both (**A**) and (**B**) there is independent change to life within sponges (**F**, **G**) with loss of the byssus. Finally, and independently, there is the infaunal habit of the Pinnidae (**H**), heteromyarians with an exceptionally large byssus.

TABLE I

Pteriacea

Family	Genus	Ligament		Byssus	Habitat		
		Alivincular	Multivincular		Epifaunal to rock, etc.	Infaunal sponges	Infaunal soft substrate
Pteriidae (Mono-myarian)							
	Pteria	x	—	x	x	—	—
	Pinctada	x	—	x	x	—	—
Vulsellidae (Mono-myarian)							
	Isognomon	—	x	x	x	—	—
	Crenatula	—	x	—	—	x	—
	Foramelina	x	—	x	x	—	—
	Vulsella	x	—	—	—	x	—
	Malleus regula	x	—	x	x	—	—
	M. malleus	x	—	x	—	—	x (coarse sand)
	M. albus (adult)	x	—	—	—	—	x (muddy sand)
(Pinnidae) (Hetero-myarian)							
	Pinna	x	—	x	—	—	x
	Atrina	x	—	x	—	—	x

Elongation in Malleus and I. isognomon

The typical monomyarian (Yonge, 1953a) is rounded with the exception of occasional species or varieties in the cemented Ostreacea and Etheriidae (Unionacea), *e.g.,* respectively, *Crassostrea gigas* and *Etheria elliptica* var. *cailliaudi* (Yonge, 1962), although in both, and especially in the latter, it is the ligamental region particularly which elongates dorso-ventrally. Among those byssally attached, elongation is confined to *Malleus* spp. and to *I. isognomon*.

The primitive condition in the Pteriacea (omitting the Pinnidae) is probably best represented by *Pinctada* and by rounded species of *Isognomon*. Unlike the Pectinacea, the visceral mass is proximal to the adductor into a dorsal embayment in which its fits (Figs. 2**A**, 8). Distal extension is thus readily attained by change

in growth gradients involving straightening and extension of the ctenidia. The difference between *I. ephippium* and *I. isognomon* (*cf.* Figs. 7 and 8) is brought about in this way and is associated with change to a vertical posture and a modified mode of life.
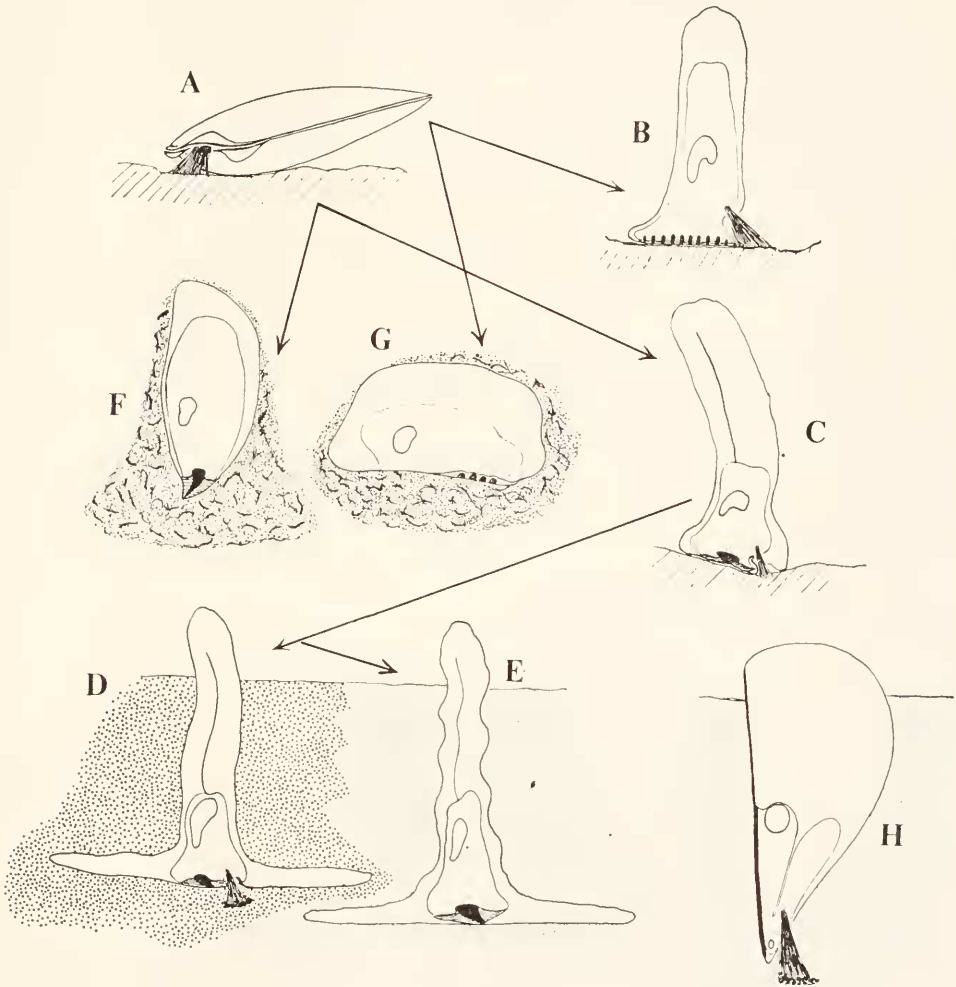

FIGURE 13. Pteriacea: drawings illustrating major adaptations and habitats of representative genera and species. **A**, *Pinctada* or *Isognomon ephippium* (alivincular and multivincular ligaments, respectively), rounded lying on right valve, byssally attached to hard substrate; **B**, *I. isognomon,* elongated, vertically disposed, byssally attached; **C**, *M. regula,* as in **B**; **D**, *M. malleus,* elongated with long hinge line, byssally attached within coarse sand; **E**, *M. albus,* as in **D** but adult not attached and in muddy sand; **F**, **G**, *Vulsella* (alivincular ligament) and *Crenatula* (multivincular ligament) both within sponges; **H**, *Pinna,* elongated, byssally attached in soft substrates.

Elongation is characteristic of the genus *Malleus*. Although, as shown in Figure 5B, the first formed shell is rounded, this is quickly altered by subsequent extensions of the mantle. The major changes involved consist of:

1. Great distal extension of the marginal prismatic zone of the shell.
2. Appearance of a pallial retractor closely associated with the elongated ctenidium.
3. Movement of byssal notch to the hinge line so that byssus emerges "downward."
4. Appearance of a promyal chamber proximal to the adductor (as in *Crassostrea*) made possible by elongation and permitting more efficient water circulation in the proximal region of the mantle cavity.
5. Development of a unique accessory foot concerned with cleansing of this region of the elongated mantle cavity.
6. Loss of any previous asymmetry associated with the recumbent posture, *i.e.,* of valves, byssal notch (gradually) and pedal musculature.

Other changes, notably elongation of the hinge line and eventual loss of the byssus, are associated with change from epifaunal to infaunal life.

Comparison between *M. regula* and *I. isognomon* has already been made (*cf.* Figs. 2 and 8). There is remarkable convergence both in form and consequent habit leading to the complete mingling of populations observed in the channel between Palau Gaya and Palau Tatagan. They are sympatric species. While the certainly more highly specialized *M. regula* might be expected to be the more successful this is certainly not the case at lower levels of the bed, over all levels of which *I. isognomon* occurs. The vertical distances are, of course, very small.

This mingling of populations of two species apparently contradicts the "competitive exclusion principle" of Gause (1934) which postulates that closely related (in this case similarly adapted) species with the same ecology cannot live together. Mayr (1963) has pointed out the exceptions, namely where two species occupy different niches in the same general habitat and the case of generalized herbivores where numbers are controlled by predators or disease and *not* by limitation of food. This could certainly apply to *M. regula* and *I. isognomon*.

The two species feed in identical ways and in shallow water where phytoplankton should be rich. Although *M. regula* is certainly the more highly adapted for dealing with collection of sediment within the vertically disposed mantle cavity this does not appear to give the species any obvious advantage over *Isognomon*. (It may well be a factor in permitting related species to exploit infaunal life.) As already noted, possible differences in settlement behavior and in resistance to limited degrees of exposure (but to *very* high temperatures) could account for the greater abundance of *M. regula* at higher, and of *I. isognomon* at lower, levels. But the major factor permitting co-existence of the two species would seem to be their different spawning seasons for which adequate evidence was obtained. In February *M. regula* had recently spawned but *I. isognomon* was only preparing to do so. There could be a gap of a month, or months, between the two events. There would therefore be no competition during the most crucial stages in the life history, when the larvae are planktonic and, above all, when they are settling with the accompanying, usually very rapid, metamorphosis into the adult form with assumption of the adult habit.

Summary

1. Study of the structure and mode of life of *Malleus regula* provides the basis for consideration of the "hammer" species, *M. malleus* and *M. albus.*

2. *M. regula* occurs byssally attached, vertically disposed on rocky substrates associated with mud and is widely distributed in the tropical Indo-Pacific.

3. The distal two-thirds of the elongated shell is exclusively prismatic. By means of special pallial retractors the mantle lobes can be withdrawn within the nacreous region.

4. The massive opisthodetic ligament has a short secondary extension of fusion layer.

5. A promyal chamber on the right side proximal to the adductor increases water flow into the exhalant chamber.

6. The long filibranch ctenidia provide a vertically extended food-collecting surface.

7. The foot is concerned with planting of the massive byssus which emerges through a notch in the right valve but on the under (*i.e.,* dorsal) surface. There is also a unique and very long accessory foot, ventrally grooved, everywhere ciliated and in constant writhing activity due to blood pressure and intrinsic muscle. Moving freely throughout the lower mantle cavity it can only be concerned with cleansing.

8. Pseudofaeces are ejected from the distal tip of the mantle cavity.

9. *M. malleus,* the black hammer shell, occurs vertically embedded in coarse sand or sandy gravel. Byssus threads are attached to fragments within the substrate. The great anterior and posterior elongations of the hinge line (also exclusively prismatic) are separated by the byssal notch (now affecting both valves).

10. Shells are usually excessively irregular due to the great exposure to damage and the almost unlimited powers of rapid repair by the three pallial extensions.

11. *M. albus,* the white hammer shell, is stouter and inhabits muddy sand. During growth it loses the byssus with reduction of the foot and byssal retractors and closure of the byssal notch. The accessory foot is not affected. The animal becomes anchored in the substrate exclusively by the anterior and posterior extensions of the shell.

12. Description of the typically rounded *Isognomon ephippium* leads to that of the elongated *I. isognomon* which occupies precisely the same habitat as *M. regula*.

13. It lacks the pallial retractors, promyal chamber and accessory foot of *Malleus*, the nacreous region is more extended distally and the ligament is multivincular (the formation of which is discussed), producing some posterior, but never any anterior, extension of the hinge line.

14. A remarkably dense mixed bed of *M. regula* and *I. isognomon* in Darvel Bay, Sabah (Borneo), is described. Different spawning periods, by preventing competition during settlement, may account for this complete intermixing of sympatric species, which, however, are generalized herbivores where numbers are not limited by food supply.

15. From a basic epifaunal habit (*Pteria, Isognomon, M. regula*), members of the Pteriacea have become adapted for infaunal life within sponges (*Vulsella, Crenatula*) or within soft substrates (*M. malleus, M. alba* and the Pinnidae).

16. There is final discussion about elongation in monomyarians, *i.e.,* in the genus *Malleus* and in *I. isognomon.*

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